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MONODONTOMERUS ARGENTINUS BRETHES (HYMENOPTERA: TORYMIDAE): A PARASITOID OF EUGLOSSA NIGROPILOSA MOURE (HYMENOPTERA: APIDAE: EUGLOSSINAE)

Euglossine bees are the only group in the subfamily Apidoideae that do not have eusocial behavior. Euglossines display a broad spectrum of social interactions, from solitary to presocial, and are thus an important group for studying the evolution of eusociability in bees (Garófalo, C. A. 1985. Entomol. Gener., 11: 77–83). An important factor involved in the origin of social behavior is the effect of parasites and parasitoids on survival and reproduction (Roubik, D. W. 1989. Ecology and natural history of tropical bees [1st ed.]. Cambridge University Press. New York).

Although it is known that microhymenoptera are parasitoids of *Euglossa* (Zucchi, R., S. F. Sakagami & J. M. F. de Camargo. 1969. J. Fac. Sci. Hokkaido Univ., Series VI, Zool., 17: 271–380), little is known about their relationship with their hosts (Dressler, R. L. 1982. Ann. Rev. Ecol. Syst., 13: 373–394). Here I present data on the parasitic behavior of the microhymenopteran *Monodontomerus argentinus* Brethes (Torymidae) and discuss its effect on the social structure of *E. nigropilosa*. I compared the percentage parasitism of *M. argentinus* on both an attended and an unattended nest of *E. nigropilosa*. This study was carried out between August 1994 and April 1995.

Euglossa nigropilosa is a communal bee of NW South America, the colonies of which have active bees all year. It is distributed between 700 and 1400 m in the Andes of Colombia and Ecuador. This species builds nests with an envelope, a resinous cover that protects the cells. Cells are of 10×6 mm, with soft resinous walls. I found several nests of *E. nigropilosa* in wood cavities of timber buildings at the Reserva Natural La Planada (RNLP), Colombia (77°24' W, 1°5' N). The nests contained colonies of up to 22 females (Otero, J. T. 1996. Bol. Mus. Ent. Univ. Valle. 4: 1–19).

Nests of *E. nigropilosa* were parasitized by *M. argentinus*, an ectoparasitic wasp that is known to attack the solitary bee *Eufriesea nigrescens* Friese, another euglossine, in the eastern part of the Andes in Colombia (Sakagami, S. F. & Strum. 1965. Insecta Matsumurana, 28: 83–97). This is the first record of a different host for *M. argentinus*. Samples of both species were deposited in the Museo de Entomología of Departamento de Biología de la Universidad del Valle (Cali, Colombia).

With the objective to study bee behavior inside the nest, on 20 Sept. 1994 I placed a nest with four adult bees and 18 cells of *E. nigropilosa* in a wooden box $30 \times 15 \times 10$ cm, with a glass plate covering the upper surface and a wood cover which remained in place during non-observation hours. The bees had free access through a one cm diameter hole. However, the adult bees abandoned the box nest. This undefended nest was compared to a nearby undisturbed nest, in which adult bees were still present, for levels of cell parasitism by *M. argentinus*.

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This second nest provided a control for the degree to which adult bees can protect their nest from parasitism. On 11 Nov. 1994 I opened all the cells of the abandoned box nest to check the level of parasitism of *M. argentinus*. For comparison, I opened 20 randomly chosen cells from the undisturbed nest to determine whether or not they were parasitized.

Comparison between the nests with and without females revealed that parasitism dropped significantly ($\chi^2 = 12.73$, P = 0.0004) with the presence of adults in the nest. The percentage of parasitism on the 18 cells in the box nest with female bees absent was 72%. However, the percentage for the control nest, which had between eight and 14 female bees, was only 15%, based on the sampled cells. In the box nest cells there was an average of 13.69 (\pm 9.04 SD, n = 13) wasp offspring per cell. Individual wasps were found at all developmental stages: young larvae, mature larvae, prepupae (pupae without pigmentation); and pupae (black pupae).

I observed the behavior of 38 *M. argentinus* wasps inside the defended *E. nigropilosa* nest. *Monodontomerus argentinus* arrived at the nest entrance after a zigzag flight. The wasp flew around the entrance for up to five min, before landing at the entrance hole. Parasitoid wasps entered the nest slowly, using the same entrance hole that the bees used. Upon landing, the wasps drummed on the surface of the nest with their antennae, moving them fast and harmoniously. The wasps alternated each antenna in this process. The wasps advanced slowly and continued drumming until they arrived at the entrance hole. Once inside the nest, the wasps drummed with their antennae on the surface of a cell for up to five min. without moving any other part of the body. When a wasp found an appropriate cell, it continued drumming for several minutes before ovipositing. Oviposition lasted for up to two min. For this process the wasp raised her abdomen, exerted her ovipositor and put it in contact with the resin wall of the cell. Occasionally the parasitoids withdrew their abdomen and continued drumming on the next cell.

Euglossa nigropilosa appeared to recognize *M. argentinus* as a natural enemy. These interactions were very strong. For example, a parasitoid, recently killed in a cyanide bottle, was left exposed in the nest. This body was torn apart by a resident bee. On first detecting the dead wasp, the bee became excited and circled around it, touching it with her antennae. It then bit the wasp in the abdomen and pushed it five cm away from the cell. The bee again found the dead wasp on the ground and bit it repeatedly for more than a minute. Following this attack the parasitoid lost two legs and had its wing and crushed abdomen nearly destroyed.

This strong reaction may, however, have been a response to the odor of the cyanide, and not the presence of the parasitoid body. During observations of attempts to parasitize a cell, I never observed the bees to perceive the wasp's presence. The wasps proved very adept at escaping from the bees notice in the nest. When a parasitoid was approached by a bee, the wasp jumped to the ground, so evading detection, and remained there for several minutes before attempting to oviposit again.

Sakagami and Strum (1965) found an aggregation of nests of the solitary bee *Euplusia longipennis* in Colombia in 1956 (*Eufriesea nigrescens* sensu Kimsey, L. S. 1982. Systematics of bees of the genus *Eufriesea*. University of California press). These nests had 81 highly elaborate resinous cells of approximately 19×9 mm, two of which were parasitized by *M. argentinus* (2.5% parasitism). Each



Table 1. Length of bees and cells, and number of broods per cell of the parasitic wasp Monodontomerus argentinus in two different euglossine bees in Colombia.

	Euglossa nigropilosa	Eufriesea nigrescens	
Bee length (mm)	12	16	
Cell length (mm)	10	19	
Cell diameter (mm)	6	8	
Number of broods by cell	13.7 (SD = 9.4; $n = 13$)	33.5 (SD = 2.1; n = 2)	

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parasitized cell had an average of 33.5 (SD \pm 2.1, n = 2) parasites. Eufriesea nigrescens and Euglossa nigropilosa were attacked by the same parasitoid, *M.* argentinus, but the two host species have different defense strategies. The solitary species, *E. nigrescens*, provides cells with thick protective walls. In contrast *E.* nigropilosa build cells with a thin, vulnerable wall. However, adult bees of *E.* nigropilosa may protect the nest from *M. argentinus*. In addition, the presence of a resinous envelope enclosing the nest may restrict the wasp's entrance. These defenses of *E. nigropilosa*, however, appear to provide less effective protection from the parasitic wasps than the thick cell walls of *E. nigrescens*. Parasitism incidence was higher in *E. nigropilosa*, between 72% in box nest and 15% in the control nest, than in *E. nigrescens* (2.5%). There appears to be less parasitism when nests are protected by many active females. In this case, the parasitoids probably spent more time escaping from resident bees and were not able to oviposit in cells.

From these observations I suggest that the presence of active bees in the nest may affect the rate of M. argentinus parasitism of E. nigropilosa. Despite having vulnerable cell walls, E. nigropilosa has active bees throughout the year and the large colony size makes the presence of a female in the nest more likely, decreasing the risk of M. argentinus attack. In contrast, E. nigrescens is a seasonal bee with oviposition limited to only two months of the year. Females of Eufriesea nigrescens die after oviposition and they can not protect the cells. Thus an intrinsic protective mechanism is needed, in this case a thick resinous cell wall that is difficult for the parasitoid to penetrate.

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